ON THE STRUCTURE AND CLASSIFICATION OF THE TREMATASPIDÆ.[1]

WILLIAM PATTEN.

Of all the families usually included in the problematical and heterogeneous group of animals called the "ostracoderms," none is more interesting to the morphologist than the Trematapidæ, as the little known about them shows they possessed a most extraordinary structure, unlike in many respects that of any other group of animals. While the character of the trunk scales, of the orbits and other sensory openings, the minute structure of the shell, and the presence of the newly discovered lateral-line system clearly indicate the affinity of Trematapis with Pteraspis, Cephalaspis, and Pterichthys, and through them with the true vertebrates, other features, such as the general shape of the shield and its more superficial texture, which have long been a source of perplexity to the paleontologist, clearly point to the affinity of Trematapis with arthropods like Limulus, Apus, and the trilobites.

The importance of the Trematapidæ to the morphologist also lies in the fact that while the specimens are rare and more or less fragmentary, they are usually well preserved and give fair promise that ultimately we shall be able to decipher in detail the structure of all their hard parts. This knowledge will certainly throw much light on the morphology of the whole group of ostracoderms, and may afford decisive evidence of the genetic relationship between the vertebrates and invertebrates.

When, therefore, through the generosity of the administration of Dartmouth College, I was granted a half-year's leave of absence, I decided to make as thorough an investigation of the ostracoderms as my time and means would allow, with the special object of determining whether any evidence could be

[1] This paper is an abstract of one about to be published in the *Memoirs of the Imperial Academy of Sciences of St. Petersburg.*

found bearing out our assumption that they are an intermediate group of animals related on one hand with the arthropods and on the other with the vertebrates. My plan was to study all the most important collections in Great Britain and the Continent and to purchase or collect material that might be used for detailed study by sectioning or by other methods, as the

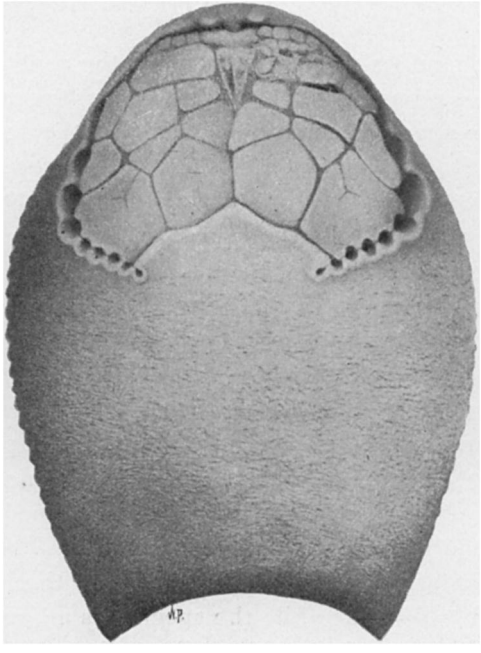

FIG. 1. — A partial reconstruction of the ventral side of the head of Trematapis. Enlarged about 2½ diameters. The figure was made from a wax model constructed after several specimens and fragments in the University and the Imperial Academy, at St. Petersburg, and in the Dartmouth College Collections.

valuable type specimens permanently preserved in museums could not be utilized in this manner.

It did not take long to discover that the following out of the second part of my program, the collection of Thyestes and of Trematapis, was a most difficult task. So far as I know, every fragment of these two genera has been taken from a shallow pit about four feet deep and covering perhaps an area of three or four hundred square yards, hidden in the heart of the remote and otherwise little-known island of Ösel in the Baltic Sea.

The mysterious treasures of this classic spot have drawn to its sides many famous scientific men from all quarters of the globe. From time to time during the last forty years or more many beautifully preserved eurypterids and an occasional Trematapis have been taken from this insignificant pit in a pasture. During the past twelve or thirteen years the spot has been

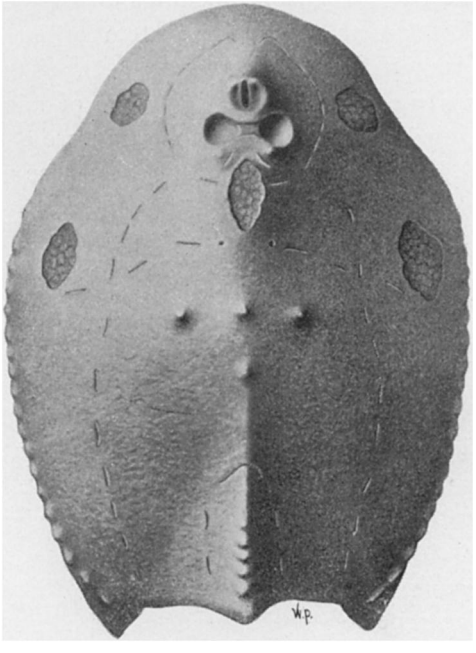

FIG. 2. — The dorsal surface of the head of Trematapis.

worked more systematically by Mr. A. Simonson, who has collected, with very few exceptions, all the material of Trematapis and Thyestes that has ever been found; and yet, with the most careful and painstaking work, and with considerable assistance from common laborers, two or three, very rarely four, fragmentary heads of Trematapis are all that reward the labors of a whole summer. I considered myself fortunate, therefore, in being able to purchase nearly all of the fossils collected by Herr Simonson during that season. The collection contained many specimens of Thyestes, Cephalaspis, and Bunodes, together with four heads of Trematapis, some of which were in exceptionally

good condition; but, unfortunately, none of the last-named genus showed the presence of the plates in the oral region.

All of these specimens have been added to the collections in Butterfield Museum of Dartmouth College.

The four heads of Trematapis (which have been cleaned with great care) have enabled me to make out several new details concerning the sensory openings on the dorsal surface; they were the first to show the system of lateral-line pits, although these pits were afterwards seen on most of the St. Petersburg specimens. But they were of special value in that they enabled me to work out the structure of the anterior margin of the dorsal shield and to discover three new openings

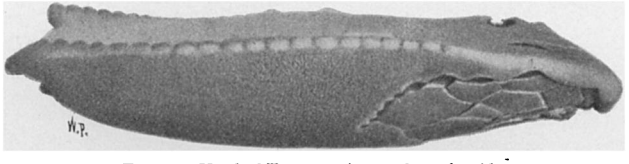

FIG. 3. — Head of Trematapis seen from the side.

in the series of so-called gill openings described by Rohon. These parts in the Petersburg material were absent or had been destroyed by rough handling.

The reconstruction of the oral region was made from a study of the single specimen and its cast that have already been described by Rohon. The original fossil had lost many details through repeated handling and the apparently incautious attempts to clean out the matrix between the edges of the plates. The original mold, however, was in nearly perfect condition, and by taking several impressions of it in dentist's wax a beautiful reproduction of the original untouched fossil was obtained, from which were worked out all the details in the arrangement of the oral plates shown in the restoration. These casts and the enlarged model are now preserved in Butterfield Museum at Dartmouth College.

Our observations on the structure of Trematapis have brought out the following principal facts:

The *Lateral-Line Organs of Trematapis* consist of a series of shallow groove-like dots and dashes, arranged in linear series on the dorsal surface of the shield. We distinguish a

circumorbital, marginal, anterior transverse, and a posterior dorsal line. The first two lines appear to correspond with the circumorbital, and the trunk line of Pterichthys. The circumorbital line is represented in Tolypaspis by a V-shaped ridge.

The Sensory Openings of the Dorsal Shield. — There are four centrally placed openings and two pairs of marginal ones on the dorsal shield of Trematapsis. Interpret these openings provisionally as follows: the posterior central opening is that of an olfactory organ; the three anterior central ones belong to the median eye; the anterior lateral openings contain the lateral eyes, and the posterior lateral pair, a segmental sense organ comparable with the dorsal organ of embryo Limuli.

The olfactory opening and both pairs of lateral openings in all well-preserved specimens possess sharply scalloped margins and a reticulated bony floor. Transverse sections show that the floor is an extension of the inner layers of the shell.

In transverse sections through the frontal depression the median slit is seen to be a true perforation of the shell, its infolded margins forming a short flattened tube.

The median orbits are separate, nearly spherical chambers, enclosed in a network of bony tissue formed by ingrowths of the inner layers of the shell. The narrow median canal that appears to connect the two orbits is closed by a deep-lying bony floor, also formed from the inner layers of the shell.

The *lateral eyes* were small and subordinate in function to the median ones. They probably occupied the anterior pair of marginal openings, the rounded incisions on the edge of the openings possibly indicating the presence of compound eyes, consisting of a few large ommatidia. The lateral eye orbits agree with those of Limulus in being shut off from the interior of the head by a bony network arising from the inner layer of the shell.

The *posterior marginal openings* agree in position with the so-called dorsal organs of Limulus, a pair of segmental sense organs serially homologous with the lateral eyes and lying in larval Limuli opposite the fourth pair of thoracic appendages.

The Median Eye. — The three anterior median openings I have compared with the triocular median eye of Limulus, Apus,

trilobites, Merostomata, and other arthropods, but not with the three frontal ocelli of adult insects. In Limulus, where the structure and development of this organ is best known, the retinas of the median ocelli arise from two pairs of segmental sense organs, that during the closing in of the brain migrate from the margins of the cephalic lobes to the roof of the fore-brain vesicle. Here the ocelli come to lie at the blind end of a long tubular outgrowth of the brain roof. The distal end of the tube then divides into two vesicles, lying in the median line, one in front of the other. The united retinas of one pair of ocelli form one of the vesicles and, at a considerably later period, lie in a degenerate condition, deeply buried beneath a median tubercle on the dorsal surface of the head. The other two retinas lie close together in the second vesicle, beneath two median lenses. These two terminal vesicles are found in a more or less modified form in many Crustacea and without doubt in the trilobites and Merostomata also, since the arrangement of their surface lenses is, in some case, precisely the same as in Limulus. The median eye of Trematapis, like that of Limulus, probably consists of a complex group of three ocelli derived from the incomplete fusion of two pairs. They were, no doubt, true cerebral eyes, lying at the end of a tubular outgrowth of the brain. The distal end of this tube was probably bifurcate, the anterior vesicle containing one pair of ocelli lying beneath, or in, the median pit and the posterior vesicle lying in the paired median orbits. The anterior and posterior vesicles of Limulus and Trematapis are represented in true vertebrates by either the vesicular ends of two separate outgrowths from the brain roof, one behind the other, or by two terminal vesicles, one in front of the other, arising from a common tubular outgrowth.

According to this view, the visual organs of vertebrates are derived from three pairs of segmental sense organs, originally situated near the margins of the cephalic lobes. The median eyes, which were the most anterior, were the first to be converted into cerebral eyes of the vertebrate type. This change took place in the arthropods, the various steps in the process being clearly seen in insects, crustaceans, and arachnids. The transfer of the lateral eyes to the cerebral vesicles and

their consequent inversion took place much later, probably in the intermediate type of animals to which the Trematapidæ belong. It was during this period that the median eyes reached their highest development and the lateral eyes degenerated or, in some cases, disappeared completely from the surface. We have no means of knowing whether their temporary decline in functional importance was the cause, or the result, of their transformation into eyes of the cerebral type.

The *postorbital opening* probably contained the forerunner of the vertebrate olfactory organ. I have identified it with the frontal organ of Limulus, Branchipus, Apus, and others. This organ in the arthropods presents extraordinary variation in its position, but can always be identified by the peculiar histological structure of the terminal organ and its nerve, and by the origin of the nerve in the brain. In Limulus, no doubt, the organ was originally a visual organ serially homologous with the lateral and median eyes. In the adult it lies on the ventral side in front of the cheliceræ. It gradually loses the histological characters of a visual organ and finally presents many points of resemblance to the olfactory organ of a vertebrate, especially in the structure and relations of its nerves. The hypostomeal eyes of trilobites are very probably homologous with the olfactory organs of Limulus. In Branchipus the same organ has moved from its original position on the ventral surface to a point on the dorsal surface almost as far back as the median ocellus. In Apus the two organs have moved still farther back and have united behind the median ocellus to form an unpaired organ in precisely the same location as the post-orbital opening of Trematapis.

The *Oral Plates* have been worked out anew from the single fossil and its cast that was used by Rohon. My description differs from his in several very important respects.

According to my interpretation of this important fossil there are on each side nine large oral plates arranged in four rows. Some of the marginal plates are provided with one or more rounded incisions lying opposite corresponding incisions of the ventral and dorsal shields. The marginal plate of the fourth row is probably a compound plate. There is a row of four or

five small plates on each side, just behind the anterior margin of the dorsal shield.

A small triangular median plate lies in the anterior oral region. Its anterior margin seems to be articulated to the hinge-like process on the anterior median margin of the dorsal shield. The outer surface of the plate is smooth and provided with a low, keel-like ridge that gives it the appearance of the rostrum of an arthropod. Its apex lies considerably below the surrounding surface in a median depression that probably leads into a small circular oral cavity like that of an arachnid. There is no trace of a large transverse oral opening, like that described by Rohon, between the anterior plates and the anterior ventral margin of the dorsal shield.

The *anterior margin of the dorsal shield* is deflected sharply downward to form a low wall in front of the oral region. A small keel lies in the middle line on the posterior surface of the wall, with its rounded edge directed backwards. Two rounded toothlike projections of the rim, directed ventrally, lie on either side. The lateral margins of the dorsal shield are folded sharply toward the ventral median line and present three large rounded incisions that must be regarded as a forward extension of the series of six incisions of the ventral shield described by Schmidt and Rohon.

The Appendages. — The most anterior incision is the largest and is clearly the same as that so well seen on the margin of the dorsal shield in Tolypaspis, Cyathaspis, and Pteraspis, and which has been regarded as an opening for the lateral eye. Lindström's important discovery of an appendage in Cyathaspis, my own discovery of fragments of the appendages in Trematapis, and a renewed examination of the pteraspids in the British Museum indicate that in these four genera the large anterior marginal incision served for the attachment of an oar-like appendage similar to that in Pterichthys and Bothriolepis. The remaining openings, which are unquestionably serially homologous with the first, must have served for the attachment of other appendages of a similar nature. They decreased in size from before backwards, and were possibly too delicate to be well preserved in a fossil condition.

The Entapophyses and the Trabeculæ.—It is doubtful whether the endolymphatic ducts of Rohon are actual perforations of the shell. In sections they are seen to be deep tubular infoldings, probably closed at the inner end. They appear to be comparable with those infoldings, or entapophyses, on the dorsal shield of Limulus which serve for the attachment of dorso-ventral muscles. This interpretation is strengthened by the fact that serial sections show the presence of another pair of bony ingrowths, just behind and in line with the so-called endolymphatic ducts. They are long deep plates that unquestionably serve for the attachment of muscles, since the frayed-out ossified tendons are still attached to their inner ends. These entapophyses are of great importance, as they indicate a similar arrangement of muscles and appendages to that seen in Limulus. They probably served for the attachment of dorso-ventral muscles, arising from the dorsal surface of the cartilaginous cranium and from the various pairs of cephalic appendages.

The presence of a similar set of muscles in Pteraspis and Cyathaspis is indicated by radiating impressions or lobes on the inner surface of the shell, similar to the radiating muscle markings on the dorsal wall of Limulus.

Transverse sections of the whole head show that the shell is specially thickened in the region of the crista occipitalis, and that the margin of the shield is considerably strengthened by a network of bony trabeculæ uniting the edges of the dorsal and ventral walls. The marginal trabeculæ are very similar to those I have described in Limulus. The marginal cells of Eukeraspis are probably produced by a special arrangement of these trabeculæ.

A loose network of bony trabeculæ is also developed round the median and lateral openings of the dorsal shield and along the incisions of the ventral wall where the appendages are attached. With the above exceptions, the inner surfaces of the dorsal and ventral shields are smooth.

The minute structure of the shell of Trematapis and other members of the ostracoderms can be best explained, as we have pointed out elsewhere, on the assumption that it is a modification of a three-layered dermal skeleton similar to that of Limulus.

The Resemblance between the Tremataspidæ and the Arthropods.—The following summary of the principal characteristics of the Trematapidæ shows how strongly they resemble the arthropods, and how surprisingly the resemblance has been strengthened at certain points by important discoveries in unexpected directions.

The Trematapidæ resemble the arthropods in (*a*) their general arthropod appearance, (*b*) in the minute structure of the shell, (*c*) in the structure and arrangement of the openings for the eyes and olfactory organs, (*d*) in the character and arrangement of the oral plates, (*e*) in the absence of vertebrate jaws and mouth and in the presence of a small centrally placed oral opening similar to that of an arachnid, (*f*) in the presence of numerous pairs of jointed appendages.

The presence of segmented appendages in Trematapis and related forms is indicated by the following evidence: (1) the presence of a pair of oarlike jointed appendages, unlike those of any true vertebrate, in Pterichthys, Bothriolepis, Cyathaspis, Pteraspis, Tolypaspis, and Trematapis; (2) the presence of a fringe of jointed and movable appendages (25–30 pairs) along the ventral margin of the trunk of Cephalaspis; (3) the presence of a pair of crushing mandibles like those of an arthropod in the head of Cephalaspis; (4) the presence in Pterichthys, Bothriolepis, and Trematapis of oral plates that appear to be movable laterally, like the jaws of an arthropod; (5) the presence in Trematapis of a series of eight other pairs of openings like the ones to which the large swimming appendages are attached; (6) the presence in Trematapis of two pairs of entapophyses which, like those in Limulus, apparently serve for the attachment of muscles moving several pairs of appendages; (7) the presence in Cyathaspis and Pteraspis of from four to six radiating grooves on the inner surface of the dorsal shield, which, like similar markings in Limulus, indicate the points of attachment of dorso-ventral muscles moving several pairs of appendages.

The concurrent testimony, from so many different and independent sources, to the fundamental similarity between the Trematapidæ and the arthropods shows very clearly that the resemblance between them is due, neither to incidental

parallelism, nor to mimicry, but to genetic relationship and community of origin. It could not have been a remote relationship, signifying merely a common origin of both types from some annelid ancestor, because the resemblance consists in the common possession of highly specialized structures characteristic of the fully established arthropod and vertebrate types.

The genetic relationship, therefore, between the Trematas-pidæ and the arthropods can mean nothing less than the derivation, through changes in structure and function, of one type from the other.

But we must not too hastily conclude that the Trematas-pidæ are true arthropods, and by transferring them from one group to the other avoid the real problem at issue. We cannot so easily ignore the profound significance their structure has for the origin of vertebrates. Their vertebrate affinities are too obvious to be denied.

It is quite out of the question to separate the Trematas-pidæ very far, either from the Cephalaspidæ on the one hand, as is conclusively shown by the similarity in the structure of their orbits, or from the Pteraspidæ and Pterichydæ on the other, as is shown by the appendages and the lateral-line markings, or from either, as is shown by the microscopic structure of the shell. The whole group must be kept together. But, as it is quite impossible to include in the arthropods a group of animals, nearly all of which have osseous dermal skeletons, and some of which have such characteristically vertebrate bodies and fins as the Cephalaspidæ and Pterichydæ, or to include in the vertebrates animals having many pairs of jointed appendages, it becomes necessary to create for them a new class, one that shall occupy a position between the true vertebrates and arthropods, and unite these two great groups into one compact phylum.

I propose for this new class the name Peltacephalata, and include in it forms like Pterichthys, Cephalaspis, Pteraspis, Trematas-pis, and related genera. The class may be provisionally characterized as follows:

The Peltacephalata were arthropod-like animals, moving about through the soft mud on the bottom of shallow waters,

in the typical arthropod position. In many cases most of the body was probably concealed, leaving only the prominent median eyes exposed. The presence of paired oarlike appendages indicates the power of free swimming, but the more or less rigid and clumsy appendages and heavily armored body could have produced little more than brief, spasmodic excursions, like those of adult Limuli and eurypterids, or jerky, intermittent flights through the water, like those of a copepod. And, just as in these examples the shape of the body and the position of the appendages in reference to the center of gravity compel the free-swimming individual to reverse the usual position of dorsal and ventral surfaces, so in the Peltacephalata the prevalence of the same conditions must have forced them, after leaving the bottom, to turn over and swim with the neural side uppermost, in the true vertebrate position. The swimming movements were probably aided in some cases by numerous small appendages on the head and trunk. Fishlike caudal fins and tail were used in swimming and in reversing the position of the dorsal and ventral surfaces.

It was not till this new method of locomotion had completely replaced the old that the eyes left the hæmal surface (their position in most adult arthropods) and returned to the neural surface of the body (their position in embryo arthropods and their permanent position in vertebrates).

The *exoskeleton* was a true dermal armor of ectodermic origin, intermediate between the type presented by Limulus and that of the more modern vertebrates. It consisted of three principal layers, the middle one containing large, more or less regular spaces or cancellæ. The matrix was strongly laminated and penetrated by numerous dentine-like tubules, or pore canals, and contained either unipolar or multipolar osseous lacunæ. The trunk was covered with rhomboidal scales or with segmentally arranged ringlike plates. The presence of a system of superficial sense organs is indicated by numerous pitlike markings arranged in linear series.

A flattened cartilaginous cranium was present, but notochord and vertebral arches were absent or rudimentary. Median and lateral eyes were enclosed in bony orbits, sometimes protected

by hard convex coverings continuous with the outer layers of the shell. The median eye was large, complex, and important functionally. It consisted of two pairs of ocelli, one pair completely united in the median line and the other nearly so. The lateral eyes were reduced in size and in functional importance. The nasal pit was unpaired and, in some cases, situated behind the median eye. The mouth was small, circular, and situated near the center of a group of oral plates. No upper and lower jaws were present.

The head of the Peltacephalata may be regarded as a modification of the cephalothorax of an arthropod ancestor, consisting of three principal groups of segments, namely: the præœsophageal, including all the parts derived from the cephalic lobes; the true thoracic segments; and the highly modified vagus segments, formed by the forward migration and their complete union with the thorax of from two to four abdominal segments. The brain, like that of vertebrates, probably consisted of three groups of neuromeres derived from these three sources.

The Peltacephalata have their nearest relatives among the known invertebrates in the Trilobita and Merostomata, having retained to a considerable extent the general shape of the body, the structure of the head, and the mode of life characteristic of these arthropods.

Sufficient data are as yet unavailable for a permanent arrangement of the Peltacephalata into orders and families, but some modifications of the old arrangement may be made to advantage. The old subdivisions into Osteostraci and Heterostraci, proposed by Lankester, should be abandoned, as they do not mark natural divisions. The discovery of heavily armored oarlike appendages in Cyathaspis and Trematapis, and their probable presence in Pteraspis and Tolypaspis, unite these genera more closely with one another and with the Pterichydæ than ever before. It is therefore inadvisable to isolate the pteraspidian section merely on the absence of multipolar bone cells, unless the Pterichthydæ are united with the remaining families under the heading Osteostraci. But such an arrangement would not sufficiently emphasize the resemblance between

the oarlike appendages of Cyathaspis, Trematapis, and Pterichthys, and the difference between these appendages and those of Cephalaspis.

Moreover, the Pteraspidæ approach the Pterichydæ more closely than do the Trematapidæ in the division of the cephalic buckler into separate plates, and in its separation into a true cephalic or rostral portion bearing the median eyes, and a thoracic one to which the oarlike appendages are attached. On the other hand, Tolypaspis, which must be placed close to Pteraspis and Cyathaspis on account of the minute structure of the shield, shows no trace of a subdivision of its dorsal shield into separate plates.

It seems to me, therefore, that we must recognize four subdivisions of the Peltacephalata of about equal value, *viz.*, the Pteraspidæ, Trematapidæ, Pterichydæ, and Cephalaspidæ. The Cephalaspidæ occupy a somewhat isolated position on account of the very peculiar shape of the head and the position and character of the appendages, although on the other hand, as shown by the connecting form Thyestes, a close relationship between Cephalaspis and Trematapis is indicated by the resemblance between their median, lateral, and postorbital openings.

The Pterichydæ and Trematapidæ are bound together more closely than before, owing to their possession of oarlike appendages, large centrally placed orbits, and to the arrangement of the so-called lateral-line organs and oral plates.

The Syncephalata. — For the great phylum of the animal kingdom formed by the union of the vertebrates and arthropods I propose the name Syncephalata. The delimitation of the Syncephalata can be only roughly determined, especially at the lower end of the phylum. The main stalk consists of the Arachnida (including the Trilobita, Merostomata), the Peltacephalata, and the Vertebrata. The point of divergence from the main stalk of such groups as the Insecta, Crustacea, and the simplified and aberrant forms, like the Ternicata, Amphioxus, Balanoglossus, and others, are of minor importance and do not concern us here.

The justification of the term Syncephalata lies in the fact that in this vast series of segmented animals the concentration

and specialization of the anterior body segments into a head region is definitely begun and completed. It is only when this group is viewed as a whole that we see these momentous structural advances in their true perspective, and can follow the endlessly varied theme that leads steadily and consistently onward toward the completion of the most complex organic structure that has ever been produced, the vertebrate head.

DARTMOUTH COLLEGE,
January, 1902.